

FAHRENHOLZ'S RULE AND RESOURCE TRACKING: A STUDY OF
HOST-PARASITE COEVOLUTION

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Fahrenheit's Rule and Resource Tracking are two hypotheses which describe host-parasite coevolution. Fahrenheit's Rule states that "In groups of permanent parasites the classification of the parasites usually corresponds directly [to] the natural relationships of the hosts," and Resource Tracking that "the parasite may track some particular and independently distributed resource on the host ... [where] we expect noncongruent host-parasite relationships."

As a test of these hypotheses, I examined approximately 20,000 chewing lice of the genus *Geomydoecus* (Mallophaga: Trichodectidae) on pocket gophers of the genus *Geomys* (Rodentia: Geomyidae). Lice were obtained from all described subspecies of the *Geomys bursarius* complex and represent 590 individual hosts from 427 localities. In addition to qualitative features, 28 morphological characters were quantified for both adult male and female lice. The *Geomydoecus* proved to be quite variable geographically; however, there was little intrapopulation variability. This geographic variation is best represented taxonomically by recognizing 8 distinct monotypic species of lice, which cluster as 2 distinct groupings: a "northern" group, composed of *Geomydoecus geomydis*, *G. illinoensis*, *G. nebrathkensis*, *G. oklahomensis*, and *G. spickai* and a "southern" group, composed of *G. ewingi*, *G. heaneyi*, and *G. subgeomydis*. In no case was a single population of pocket gophers parasitized by more than one species of *Geomydoecus*.

Because the pocket gophers are distributed allopatrically, and together with their chewing lice have limited dispersal ability, the *Geomys*-*Geomydoecus* system is consistent with Fahrenheit's Rule. Bird ectoparasites have greater opportunity

than mammal parasites to disperse to new species of hosts, and because of the complexity of feathers, have a greater range of niches available. Therefore, the ectoparasite fauna of birds is more diverse than that of mammals and that diversity is best explained by Resource Tracking. Coevolutionary relationships are greatly affected by the dispersal of parasites among host species. Fahrenholz's Rule and Resource Tracking are not conflicting hypotheses, but represent the ends of a continuum of dispersal opportunities and niche availability.

Thus, the species of Mallophaga on *Geomys* represent a lineage that has evolved in parallel with the pocket gophers (Fahrenholz's Rule), and the distribution and taxonomic relationships of the lice are a useful tool for elucidating the relationships of the pocket gophers. Based on this relationship several hypotheses are proposed concerning the relationships of the pocket gophers.

INTRODUCTION

The hypothesis that the natural classification of certain groups of parasites parallels that of their hosts was first proposed by Fahrenholz in the late 1800's. Fahrenholz's conclusions on the phylogenetic parallelism of parasites and hosts were based on work on feather mites (Acarina), and later hypothesized that such a relationship held for the sucking lice (Anoplura) and chewing lice (Mallophaga). Eichler (1948, p. 599) subsequently coined the term "Fahrenholz's Rule" and defined this hypothesis as follows: "In groups of permanent parasites the classification of the parasites usually corresponds directly with the natural relationships of the hosts."

The basis of the hypothesis is the assumption that, at some point in the evolutionary history of host and parasite, the ancestral parasite enters a close association with the ancestral host, after which both evolve and speciate together. Thus, speciation and degree of divergence in the host taxa are parallel to those of their parasites. Although it has been suggested that the classification of various ectoparasites may be utilized as a taxonomic tool in the classification of their

vertebrate hosts (Clay, 1970; Hopkins, 1949a, b; Rothschild and Clay, 1957), little work has actually been done along these lines (Timm, 1975).

Wenzel et al. (1966) and Machado-Allison (1967) drew similar conclusions concerning the relationships of certain phyllostomatid bats, based on parasite relationships. They suggested that the vampire bats, then recognized as a family, Desmodontidae, were most closely related to the phyllostomatid bats, and that the Chilonycterinae, then a subfamily of Phyllostomatidae, should be elevated to familial status. Subsequent systematic studies of the vampire bats confirmed this and reduced the desmodontids to a subfamily of the Phyllostomatidae (Forman et al., 1968), and elevated the Chilonycterinae to familial status as the Mormoopidae (Smith, 1972). Holland (1958; 1963) proposed two hypotheses concerning the taxonomy of arctic ground squirrels, *Spermophilus parryi*, based on the taxonomy and distribution of their parasitic fleas that can be explained by: 1) a close affinity between the New World and Old World arctic ground squirrels; and 2) a distinct arctic-subarctic division in the New World ground squirrels. Nadler and Hoffmann (1977) later concluded that northern and southern populations of New World arctic ground squirrels are more similar to the Siberian ground squirrels than either is to the other.

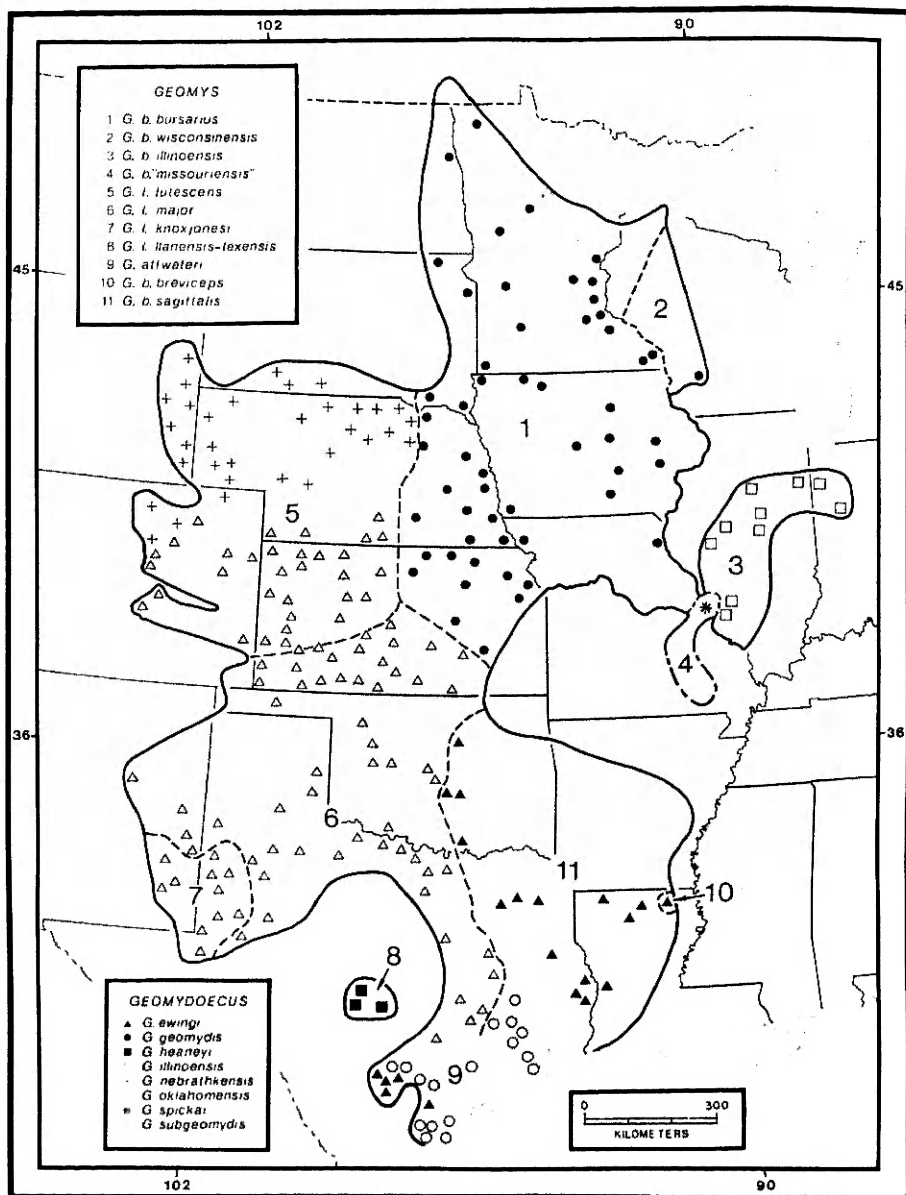
A second and contrasting model of host-parasite coevolution, is Resource Tracking. Here "...the parasite may track some particular and *independently* distributed resource on the host. Here we expect noncongruent host-parasite relationships" (Kethley and Johnston, 1975, p. 232). This hypothesis was based on a revision of the quill mites (Syringophilidae) of birds (Kethley, 1970). The Resource Tracking model predicts that there is no direct parallel relationship between the taxonomy of hosts and that of their parasites, but rather that

the parasites are tracking a resource, such as a particular type of skin, hair, feathers, quill wall thickness, etc. on the host or hosts. Resource availability then is the limiting factor controlling the occurrence of parasites on various species of hosts. In support of the Resource Tracking theory, they demonstrated that taxonomy at the generic level of the syringophilid mites does not correlate directly with the taxonomy of their bird hosts; closely related genera of mites are found on birds of different orders. They concluded that the major patterns of syringophilid inter-relationships are independent of the major patterns of host inter-relationships. In a study of the alcid lice, Eveleigh and Amano (1977) found little correlation between host relationships and parasite relationships and concluded that Resource Tracking best described their observations.

While analyzing evolutionary patterns of parasites and their hosts, I became interested in the contradictions between Fahrenholz's Rule and Resource Tracking (Timm, 1979) and saw these apparent contradictions as central to our understanding of parasite evolution. It appeared that coevolutionary relationships can be greatly affected by the dispersal of parasites from one host species to another. The unstated assumption behind Fahrenholz's Rule is that there is no gene flow of parasites between unrelated hosts. The implicit assumption behind the Resource Tracking model is that it is equally likely for all species of parasites to disperse to any host, and that at least some of those dispersers will survive and reproduce on the new host. Examples chosen from highly mobile hosts with frequent interspecific contact like communal

FIGURE 1. *An adult female plains pocket gopher, Geomys bursarius.*





birds or bats, could be misleading, especially if different parasite species possess different dispersal abilities. Yet most examples used to support individual models are from the parasites of birds and bats. The dispersal potential of the parasites does not figure explicitly in either hypothesis of host-parasite coevolution.

To test the Fahrenholz's Rule and Resource Tracking hypotheses, I chose to examine the chewing lice of the genus *Geomydoecus* (Mallophaga: Trichodectidae) on pocket gophers of the genus *Geomys* (Rodentia: Geomyidae). All five genera of the family Geomyidae are parasitized by chewing lice of the genus *Geomydoecus*. Fifteen species of *Geomydoecus* are recognized from *Geomys* (Timm, 1979; Timm and Price, 1980).

Pocket gophers of the genus *Geomys* are found throughout much of the prairie region of central North America. *Geomys* ranges from Georgia and Florida west to New Mexico, and from extreme southern Manitoba south to Tamaulipas. Currently *Geomys* is divided into nine species with some 23 subspecies, but this classification is in a current state of flux and the status of several species and subspecies is uncertain (Heaney and Timm, 1983; Honeycutt and Schmidly, 1979). The most widely distributed species of *Geomys*, *G. bursarius* (fig. 1), is found throughout much of the midwestern United States. It ranges from Illinois and Indiana west to Colorado and New Mexico, and from extreme southern Manitoba to southern Texas (fig. 2). Regarded as a single species for the past 30 years, *Geomys bursarius* is composed of populations originally described as

FIGURE 2. Map of the distribution of the 8 species of *Geomydoecus* that parasitize *Geomys attwateri*, *Geomys breviceps*, *Geomys bursarius*, and *Geomys lutescens*. The inner lines (dashes represent the boundaries between taxa of pocket gophers.

four distinct species: *Geomys bursarius* (Shaw), *Geomys breviceps* Baird, *Geomys lutescens* Merriam, and *Geomys texensis* Merriam. Recent studies have shown that there is little or no gene flow between several of the supposed subspecies of *Geomys bursarius* (Bohlin and Zimmerman, 1982; Heaney and Timm, 1983). Thus, some populations of *Geomys bursarius* form genetically distinct populations; hence, in this paper I will refer to these pocket gophers as the *Geomys bursarius* complex.

The *Geomys-Geomydoecus* host-parasite system offers opportunities for investigating the Fahrenholz's Rule and Resource Tracking hypotheses because: 1) species of *Geomys* are distributed either allopatrically or parapatrically, no species are sympatric, and 2) both the pocket gophers and their lice have extremely limited dispersal ability. Thus, the patterns observed are quite likely the primary pattern of parasite-host coevolution and not a result of secondary or tertiary recolonization. Additionally, this host-parasite system is unique in that the morphological species concept utilized for the classification of the lice was tested in the field and found to represent reproductively isolated populations (Timm, unpubl.).

METHODS

Lice were obtained from all species and subspecies of *Geomys* currently recognized, as well as from nine no longer recognized subspecies. Large samples of lice were obtained whenever possible from numerous localities throughout the range of each subspecies of pocket gopher, and are deposited in the entomology collection of the University of Minnesota, St. Paul. Pocket gophers are deposited in the Bell Museum of Natural History at the University of Minnesota, Field Museum of Natural History, Museum of Natural History at the University of Kansas, and the Museum of Zoology, University of Michigan.

Qualitative features and 28 morphological characters were quantified for adult male and female lice. Three BMDP programs were utilized for the multivariate statistical analysis: principal components analysis (BMDP4M), discriminant function analysis (BMDP7M), and cluster analysis (BMDP2M) (Timm and Price, 1980). All taxonomic decisions concerning the lice were made independently of the taxonomy and distributions of the pocket gophers; for details concerning the taxonomic revision of the pocket gophers, see Heaney and Timm (1983). Approximately 20,000 lice from some 600 individual hosts of the *Geomys bursarius* complex, representing 427 separate localities have been examined. The abundance of this material has permitted a thorough revision of the *Geomydoecus* on the *Geomys bursarius* complex and resulted in redescription of the four previously recognized species of lice, description of four additional species, and refinement of our knowledge of the distribution of lice on pocket gopher taxa (Timm, 1979; Timm and Price, 1980).

EVOLUTION AND NATURAL HISTORY OF POCKET GOPHER LICE

Evolution

Osborn (1891) was the first to mention finding lice on pocket gophers; he described *Trichodectes geomydis* on the basis of several specimens off the plains pocket gopher, *Geomys bursarius* (Shaw), from Ames, Iowa. In the next 30 years, four additional species of lice, *Trichodectes californicus* Chapman, *T. expansus* Duges, *T. scleritus* McGregor, and *T. thomomys* McGregor were described. Later, Ewing (1929) described a new genus, *Geomydoecus*, within the family Trichodectidae for this group of lice.

In 1897, Chapman described *Trichodectes californicus* on

the basis of a single female obtained from a pocket mouse, *Perognathus* sp. The erroneous designation of *Perognathus* as the host for *Geomydoecus californicus* caused a good deal of confusion because the family Geomyidae, which includes all the pocket gophers, and the family Heteromyidae, which includes the genus *Perognathus*, are closely related, leading one to expect to find closely related lice on the two families (i.e. see Jellison, 1942; Paine, 1912). However, the heteromyid rodents are parasitized by lice of the order Anoplura (genus *Fahrenholzia*), whereas the geomyids are parasitized by lice of the order Mallophaga (genus *Geomydoecus*). Werneck (1945) obtained numerous individuals of *Geomydoecus californicus* from Botta's pocket gopher, *Thomomys bottae bottae* (Eydoux and Gervais) and designated that gopher as the type host of *G. californicus*. It is now well established that all members of the genus *Geomydoecus* are obligatory ectoparasites of pocket gophers. There is no evidence to indicate that *Geomydoecus* can reproduce on hosts other than pocket gophers.

The family Geomyidae is a strictly New World family of the rodent suborder Sciuromorpha. There are five genera, found across most of the western two-thirds of North America, from central Canada south to northern Colombia. All genera of pocket gophers are parasitized by one or more species of *Geomydoecus*. The family Geomyidae is the only family of the suborder Sciuromorpha parasitized by Mallophaga; all other sciuromorphs are parasitized by anoplurans.

Currently, 102 specific and subspecific taxa are recognized in the genus *Geomydoecus*. These are morphologically divided into two distinct subgenera (see Price and Emerson, 1972). The nominate subgenus is found on all five genera of pocket gophers, whereas, the subgenus *Thomomydoecus* is found only on pocket gophers of the genus *Thomomys*.

It seems likely that the host-parasite association between *Geomydoecus* and the geomyids began at least as early as the late Miocene or early Pliocene if Russell's (1968) phyletic tree of the geomyids is correct. Geomyids probably had their origin in the southwestern United States and northern Mexico, then radiated out in all directions. Russell (1968) postulated that *Thomomys*, the most divergent genus of geomyids, split off from the main line of geomyids in the early Pliocene. It seems likely then, that this early Pliocene split in the hosts resulted in the two distinct subgenera of *Geomydoecus* we see today. However, all *Thomomys* are also parasitized by members of the subgenus *Geomydoecus* in addition to some having *Thomomydoecus*. This probably is a result of a secondary reinfestation, as these lice (subgenus *Geomydoecus*) on *Thomomys* are very similar to those on the genera *Geomys* and *Pappogeomys*. *Geomydoecus* is similar morphologically to two widespread genera of carnivore lice, *Trichodectes* and *Neotrichodectes*. Trichodectid lice are common and widespread on carnivores, but are not found on sciuromorph rodents other than geomyids. Therefore, it seems probable that the ancestral geomyids were infested with trichodectid lice from an ancestral carnivore.

Natural History

No individual or population of *Geomys* has ever been found to be parasitized by more than one species of *Geomydoecus*. The population of lice on an adult *Geomys* varies seasonally, but averages over 500 individuals during the summer months, with some individual gophers having as many as 2,000 lice. There is usually a one to one sex ratio (tables 1 and 2), but two parthenogenetic species have been found (Price and Timm, 1979). All stages of lice, including eggs, are most abundant

Table 1. Species of *Geomydoecus* in which the sex ratio of adults was significantly different than 1 to 1.

Species	Ratio	N	Significance		Source of Data
	F:M		χ^2	p	
birneyi	1.6:1	253	5.98	$p < .05$	Price & Hellenthal, 1980c
crovelloi	.7:1	647	8.20	$p < .005$	Price & Hellenthal, 1981a
expansus	.9:1	2,907	5.83	$p < .05$	Price & Hellenthal, 1975a
idahoensis	1.3:1	416	9.74	$p < .005$	Price & Hellenthal, 1980a
mobilensis	191:0*	191	-	-	Price, 1975
musculi	1.7:1	412	12.63	$p < .005$	Price & Hellenthal, 1981b
nayaritensis	2.5:1	97	8.66	$p < .005$	Price & Hellenthal, 1981b
scleritus	500:1	1,000	500.00	$p < .001$	Price & Timm, 1979
tamaulipensis	20:1	42	17.19	$p < .001$	Price & Hellenthal, 1975b
thomomys	2.1:1	308	18.94	$p < .001$	Price & Emerson, 1971

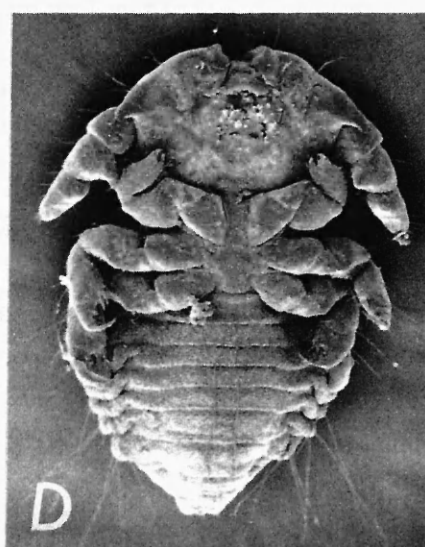
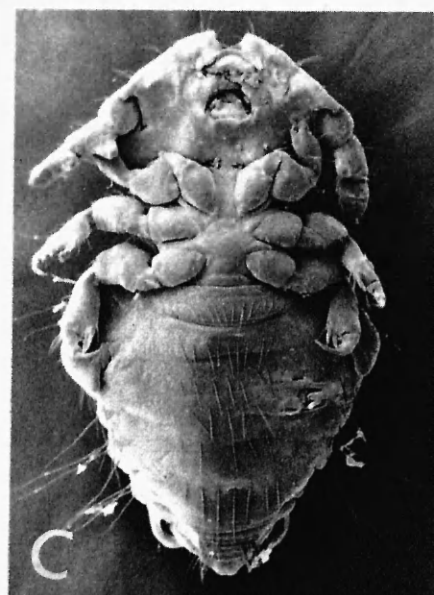
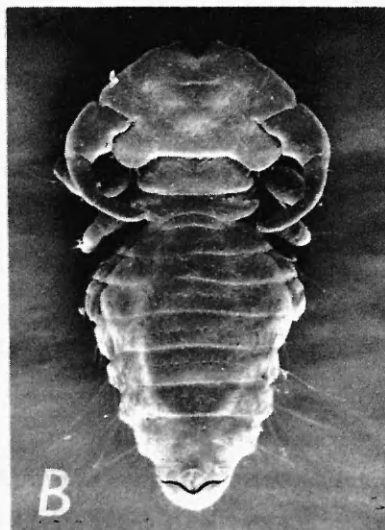
* Males of *G. mobilensis* are unknown.

Table 2. Species of *Geomydoecus* with a 1 to 1 sex ratio. Data from Price and Emerson, 1971; Price and Hellenthal, 1975a, b, 1976, 1979, 1980a, b, c, d, 1981a, b; Price and Timm, 1979; Spicka, 1981; and Timm and Price, 1980.

actuosi <i>N</i> = 897	limitaris tolteci <i>N</i> = 362
albati <i>N</i> = 414	martini <i>N</i> = 606
angularis <i>N</i> = 192	mcgregori <i>N</i> = 137
asymmetricus <i>N</i> = 52	merriami <i>N</i> = 49
aurei aurei <i>N</i> = 543	mexicanus <i>N</i> = 40
aurei grahamensis <i>N</i> = 607	minor <i>N</i> = 2,797
bajaiensis <i>N</i> = 204	neocopei <i>N</i> = 36
californicus <i>N</i> = 1,309	oklahomensis <i>N</i> = 601
centralis <i>N</i> = 3,574	oregonus <i>N</i> = 84
chapini <i>N</i> = 38	orizabae <i>N</i> = 53
chihuahuae <i>N</i> = 112	panamensis <i>N</i> = 290
clausonae <i>N</i> = 504	pattoni <i>N</i> = 20
cliftoni <i>N</i> = 65	polydentatus <i>N</i> = 43
copei <i>N</i> = 113	shastensis <i>N</i> = 456
coronadoi <i>N</i> = 40	spickai <i>N</i> = 4,835
costaricensis <i>N</i> = 38	subcalifornicus <i>N</i> = 4,755
dakotensis <i>N</i> = 81	subnubili <i>N</i> = 872
dickermani <i>N</i> = 127	texanus tropicalis <i>N</i> = 61
expansus <i>N</i> = 2,907	timmi <i>N</i> = 330
extimi <i>N</i> = 88	tolucaae <i>N</i> = 124
fulvi <i>N</i> = 193	traubi <i>N</i> = 58
genowaysi <i>N</i> = 855	truncatus <i>N</i> = 30
geomydis <i>N</i> = 984	umbrini <i>N</i> = 310
guadalupensis <i>N</i> = 166	ustulati clarkii <i>N</i> = 219
heaneyi <i>N</i> = 173	ustulati ustulati <i>N</i> = 532
hoffmanni <i>N</i> = 101	wardi <i>N</i> = 75
hueyi <i>N</i> = 387	warmanae <i>N</i> = 2,073
illinoensis <i>N</i> = 4,300	welleri welleri <i>N</i> = 2,016
jaliscoensis <i>N</i> = 100	welleri multilineatus <i>N</i> = 1,013
johnhafneri <i>N</i> = 112	williamsi <i>N</i> = 32
limitaris halli <i>N</i> = 116	yucatanensis <i>N</i> = 101
limitaris limitaris <i>N</i> = 561	zacatecae <i>N</i> = 686

on the back of the head and nape of the neck, presumably because these areas are the most difficult for the gopher to reach while grooming. Grooming by the host probably is the main factor controlling densities of louse populations. The lice probably feed on scrapings of skin and hair from their hosts. Each individual egg, called a nit, is glued to a single hair; eggs hatch in approximately 10 days, with three nymphal stages lasting about 10 days each (Rust, 1974). Rust (1974) reported that *Geomydoecus oregonus* on *Thomomys bottae* in the Sacramento Valley of California reproduced throughout the year, as did their hosts, and that adult lice lived for 30 days. Price and Timm (1979) reported that *Geomydoecus scleritus*, a parthenogenetic species on pocket gophers in the southeastern United States reproduced throughout the year, as did the host population of pocket gophers. On northern *Geomys*, lice reproduce only during the spring, summer, and early fall, and the adults live several months. The northern populations of pocket gophers reproduce only during the spring and summer months. It seems likely that these lice are cueing in on the reproductive cycle of their hosts. The only ectoparasites reproducing synchronously with their hosts are species that feed directly on blood (see Foster, 1969; Rothschild and Ford, 1964, 1966, 1969), where the reproductive steroids of the host presumably trigger the reproductive steroids of the parasite. However, pocket gopher lice feed

FIGURE 3. Pocket gopher louse, *Geomydoecus geomydis*. A. Dorsal view of an adult female; B. dorsal view of an adult male; C. ventral view of an adult female; D. ventral view of a second instar. All specimens from *Geomys bursarius bursarius*, Washington County, Kansas. Length of A and C 1.3 mm, B 1.4 mm, and D 0.9 mm.



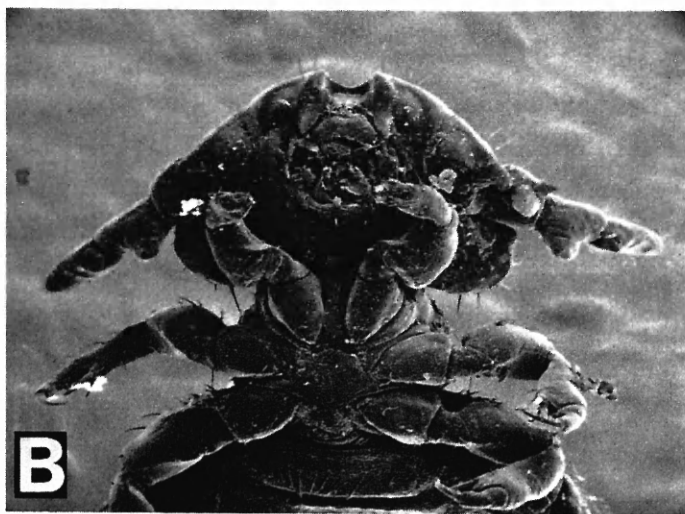
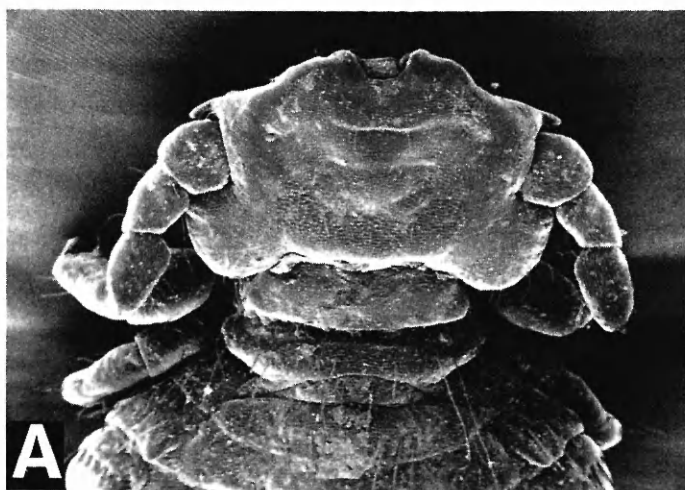
on dead tissue and not on blood. Hence, how they are cueing in on the reproductive cycle of the host is an interesting question.

Transmission of lice from one host to another occurs only upon direct contact between hosts, because lice, unlike other ectoparasites such as fleas and ticks, cannot live independently of the host. Because pocket gophers are fossorial and solitary, transmission may occur only during breeding or from a female to her offspring. I have found lice on 14 day old gophers, the approximate age when pocket gophers begin to develop a full pelage. A recently-dispersed young pocket gopher (*Geomys bursarius wisconsinensis*) which I captured had a population of over 350 lice, (*Geomydoecus geomydis* see figs. 3 and 4), including all stages of the life cycle; apparently dispersing gophers carry with them a founder population of lice.

There are few reports of *Geomydoecus* on hosts other than pocket gophers (see Timm and Price, 1980, for a review). These are presumed to be cases of stragglers or contamination because all have been single individuals and not populations. The five records of *Geomydoecus* found on long-tailed weasels, *Mustela frenata*, probably represent natural stragglers (see Timm and Price, 1980). Long-tailed weasels are major predators on pocket gophers, and probably picked up the lice from their prey.

Taxa of *Geomydoecus* are distinguished by morphology of the genitalia for both sexes, by differences in chaetotaxy,

FIGURE 4. Enlarged dorsal (A) and ventral (B) views of the head of an adult female *Geomydoecus geomydis*; width of the head 0.46 mm. Locality and host data same as in fig. 3.



size, and by the distinctive antennal scape of the males. Thus, it is likely that the morphospecies are either a subset or an aggregate of the biological species. As a test of interbreeding (or lack of it) between morphospecies of *Geomydoecus*, the systematics of lice on populations of hybridizing pocket gophers was investigated. Data from two zones of hybridization in which the two parental populations of pocket gophers each had a different species of louse were obtained. In no cases were hybrid lice found; the morphospecies of *Geomydoecus* appear to be either true host-specific biological species, or aggregates of a biological species.

DISTRIBUTION OF LICE

The *Geomydoecus* on the *Geomys bursarius* complex cluster into two main groupings, the "northern group" and the "southern group" (Timm and Price, 1980). The "northern group" is composed of the "*geomydis*" complex and the "*oklahomensis*" complex of species; the "southern group" is composed of three species (see fig. 5).

Northern Group

I. *Geomydis* complex.

A) *Geomydoecus geomydis*--This louse is found on two subspecies of pocket gophers, *Geomys bursarius bursarius* (including *majusculus*) and *Geomys bursarius wisconsinensis*.

Heaney and Timm (1983) found a continuous clinal pattern of variation in both size and cranial characteristics (fig. 6) between the northern-most populations of *Geomys bursarius bursarius* and the southern-most populations described as *Geomys bursarius majusculus* in specimens of *Geomys* from Iowa, Kansas, Minnesota, Missouri, and Nebraska. We therefore

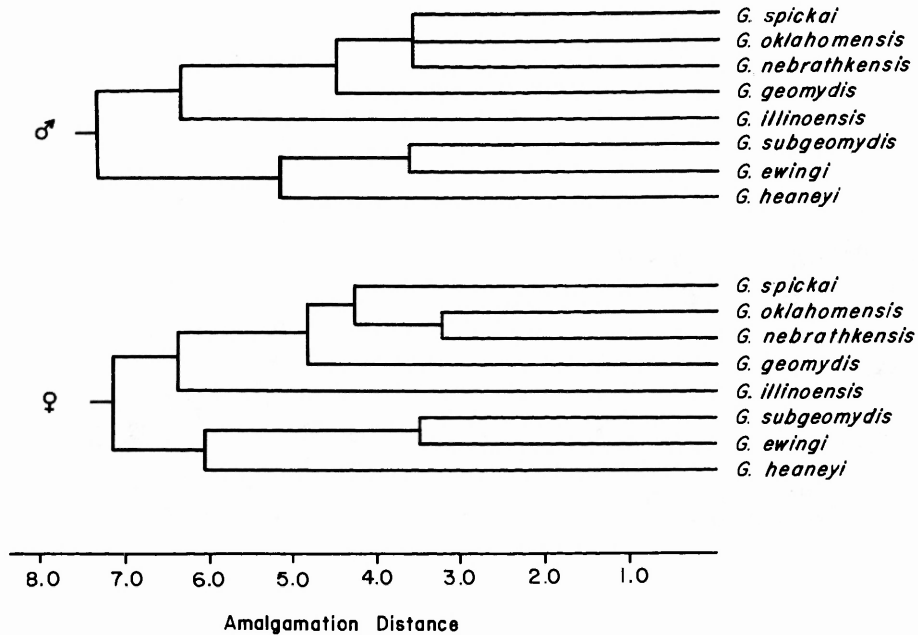
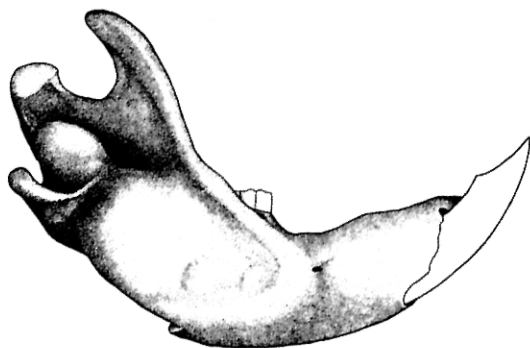
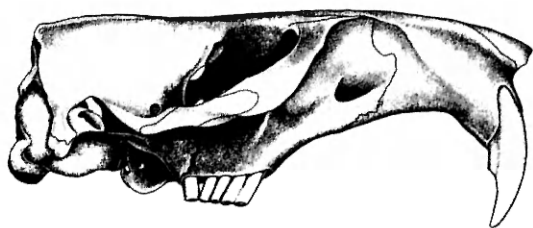
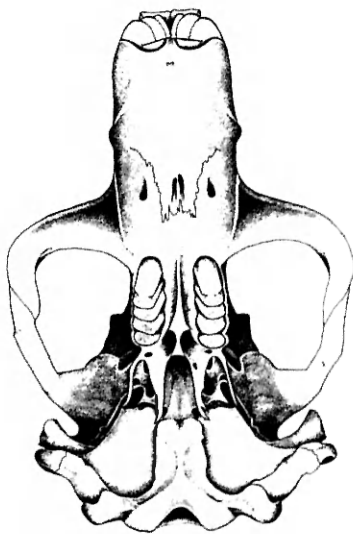
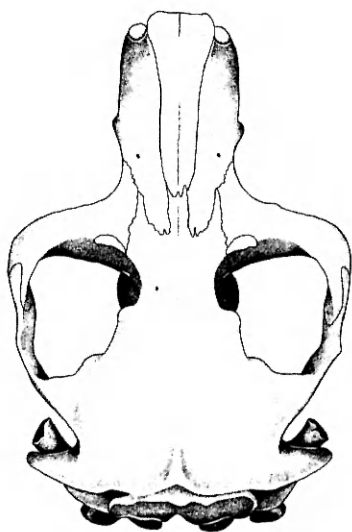


FIGURE 5. Distance phenogram of the cluster analysis of the 8 species of *Geomydoecus*. (From Timm and Price, 1980. Reprinted, with permission, from the *Journal of Medical Entomology*).

concluded that *Geomys bursarius majusculus* does not merit subspecific distinction. *Geomys bursarius wisconsinensis* (including a series from the type locality at Lone Rock, Richland Co., Wisconsin) is similar to *Geomys bursarius bursarius*, except for minor cranial characters mentioned by Jackson (1957) in his subspecific description of *Geomys bursarius wisconsinensis*. *Geomys bursarius bursarius* and *Geomys bursarius wisconsinensis* are chromosomally indistinguishable, each having $2N = 72$, $FN = 72$, and X as a large acrocentric chromosome (Hart, 1978). The karyotype of *majusculus* from eastern Kansas is similar except that FN is 70. These subspecies of pocket gophers occupy the northeastern third of the range of *Geomys bursarius*. They are found in the



Bluestem prairie (*Andropogon-Panicum-Sorghastrum*), Oak savanna (*Quercus-Andropogon*), and the Bluestem-Oak-Hickory savanna (*Andropogon-Quercus-Carya*) vegetational communities (see K  chler, 1964). Undoubtedly these pocket gophers are a closely related group.

B) *Geomydoecus illinoensis*--This species is restricted to one subspecies of pocket gopher, *Geomys bursarius illinoensis*. Although definitely a member of the "geomydis" complex, this louse is quite distinct from *Geomydoecus geomydis*, suggesting that the two populations have been separated for a considerable period of time. Its host, *Geomys bursarius illinoensis*, is the northeastern-most subspecies of *Geomys* and is unique among *Geomys* in that nearly all specimens are black.

Hart (1978) found that *illinoensis* and *majusculus* have identical karyotypes, each having $2N = 72$, $FN = 70$, and all chromosomes, including the X, are large acrocentrics. The karyotypes of *Geomys bursarius bursarius* and *Geomys bursarius wisconsinensis* are similar, but have an FN of 72 rather than 70. Cranial morphometrics suggest that *Geomys bursarius illinoensis* is a distinct subspecies most like the *Geomys bursarius bursarius* and *Geomys bursarius wisconsinensis* group, and that these two groups are distinct from the western and southern *Geomys* (Heaney and Timm, 1983). *Geomys bursarius illinoensis* occurs throughout central Illinois and extreme northwestern Indiana in the Bluestem Prairie (*Andropogon-Panicum-Sorghastrum*) - Oak-Hickory Savannah (*Quercus-Carya*) vegetational community, and is isolated geographically from

FIGURE 6. Cranium and mandible of an adult male plains pocket gopher, *Geomys bursarius*, from Oakdale, Antelope County, Nebraska (FMNH 123429). Length of skull 59.2 mm, of mandible 43.9 mm.

the more western subspecies by major river systems, the Mississippi and Illinois rivers on the west and the Kankakee River on the north.

II. *Oklahomensis* complex.

A) *Geomydoecus oklahomensis*--This louse is found on *Geomys lutescens knoxjonesi*, *Geomys lutescens lutescens* (in part), and *Geomys lutescens major* (including *industrius* and *jugossicularis*). The pocket gophers from southwestern Nebraska, western Kansas, Oklahoma, and Texas, and eastern Colorado and New Mexico are all parasitized by this species. Although this louse is the most variable and the most widely distributed of the eight species found on the *Geomys bursarius* complex, there is no evidence that any of the populations warranted classification as a distinct taxon. Principal components analysis and discriminant function analysis suggest that the lice on two populations of pocket gophers, described as *industrius* and *jugossicularis*, are a single population. Geographic variation between populations of *Geomydoecus* is evident between all other subspecies of the *Geomys bursarius* complex.

These pocket gophers have had a varied taxonomic history (Merriam, 1890, 1895; Villa and Hall, 1947; Russell and Jones, 1956; Jones, 1964; and Heaney and Timm, 1983). *Geomys lutescens* was first described from the Sand Hills of Nebraska as a subspecies of *Geomys bursarius*, but later elevated to full specific rank by Merriam. Merriam's species *lutescens* included the pocket gophers now considered *Geomys lutescens knoxjonesi*, *Geomys lutescens lutescens*, and *Geomys lutescens major*; and five other populations that are no longer considered valid subspecies, *Geomys lutescens hylaeus* Blossom, *Geomys [bursarius] industrius* Villa and Hall, *Geomys lutescens jugossicularis*

Hooper, *Geomys lutescens levisagittalis* Swenk, and *Geomys lutescens vinaceus* Swenk. Villa and Hall (1947) reduced *lutescens* to a subspecies of *Geomys bursarius* on the basis of supposed intergradation between the two populations; however, there is no intergradation between these populations (Heaney and Timm, 1983). Karyotypic variation in several populations of *Geomys* from western Texas and eastern New Mexico has been partially described (see Baker et al., 1973; Baker and Genoways, 1975; Hart, 1978), resulting in the description of a new subspecies, *Geomys [bursarius] knoxjonesi*. However, karyotypic variation in the more northern populations remains poorly understood (see Hart, 1978; Heaney and Timm, 1983; Timm et al., in press). In a recent revision, Heaney and Timm (1983) concluded that: 1) there is no justification for recognizing *industrius* and *jugossicularis* as subspecies distinct from *major*; 2) that the group of pocket gophers represented by *lutescens* and *major* is composed of closely related taxa; 3) there is little or no gene flow between *lutescens-major* and the group including *bursarius*, *illinoensis*, and *wisconsinensis*; and 4) these two groups are two distinct species.

The suggestion made by Baker and Genoways (1975) that *Geomys [bursarius] knoxjonesi* is most closely related to the *llanensis-texensis* group is unlikely for two reasons. First, their phenogram and two-dimensional projection of the cranial morphology of the gophers indicates that *knoxjonesi* is morphologically close to the *Geomys lutescens major* group. Second, *Geomys lutescens knoxjonesi* is parasitized by *Geomydoecus oklahomensis*, a member of the "northern" species group (Timm and Price, 1980) which is also found on *Geomys lutescens major* and *Geomys lutescens lutescens*. The populations of lice on *Geomys lutescens knoxjonesi* show some morphological differentiation from the main body of *Geomydoecus oklahomensis*, but

this difference is not sufficient to warrant taxonomic distinction (Timm and Price, 1980). However, *Geomys lutescens llanensis* and *Geomys lutescens texensis* have a distinctive species of louse, *Geomydoecus heaneyi*, that is a member of the "southern" species group. *Geomydoecus oklahomensis* is restricted to those taxa of *Geomys* that are found in the short-grass and mixed grass prairies, which include the Bluestem grama prairie (*Andropogon-Bouteloua*) and Grama-Buffalo grass prairie (*Bouteloua-Buchloe*). These gophers previously included in Merriam's species *lutescens* are parasitized by closely related members of the "oklahomensis" complex (*Geomydoecus oklahomensis* and *G. nebrathkensis*) and all of those gophers occurring south of the Platte River are parasitized by *Geomydoecus oklahomensis* proper.

B) *Geomydoecus nebrathkensis*--Although this species is found only on one subspecies of pocket gopher, *Geomys lutescens lutescens*, it is not found throughout its range; it occurs on the pocket gophers north of the Platte River in northern Nebraska, northeastern Colorado, eastern Wyoming, and southern South Dakota.

Hart (1978) reported that *Geomys [bursarius] lutescens* was the most variable of the subspecies of *Geomys [bursarius]* that he karyotyped, with the FN ranging from 70-98. He did find, however, that the karyotype of a single female from Kansas (south of the Platte River) was identical to those of *industrius* and *major*, while those from north of the Platte River were quite different, having numerous banded autosomes and a large metacentric X chromosome. On the basis of cranial morphology, Heaney and Timm (1983) agreed that *Geomys lutescens lutescens* was extremely variable geographically, but concluded that there was inadequate justification for splitting *lutescens* until their cytogenetics are better understood. *Geomydoecus*

nebrathkensis occurs on the *Geomys lutescens lutescens* north of the Platte River in the Nebraska Sandhills prairie (*Andropogon-Calamovilfa*), Grama-buffalo grass (*Bouteloua-Buchloe*), and Wheatgrass-bluestem-needlegrass (*Andropyron-Andropogon-Stipa*) grassland communities of Kuchler (1964).

C) *Geomydoecus spickai*--This louse is found on only one previously recognized subspecies of pocket gopher, *Geomys bursarius missouriensis*.

In his paper describing *Geomys bursarius missouriensis* as a distinct subspecies, McLaughlin (1958) stated that "The pocket gophers in Missouri represent a zoogeographical enigma ... The population of *G. b. missouriensis* is separated geographically from other populations of *G. bursarius* by a wide hiatus on the north, west and south. Only on the east does it approach the radically different *Geomys bursarius illinoensis*, which occupies the opposite bank of the Mississippi River..." Heaney and Timm (1983) found the taxa originally described as *Geomys bursarius missouriensis* to represent a composite of two different species, *Geomys bursarius* and *Geomys lutescens*. Those pocket gophers just south of the Missouri River were not significantly different from the pocket gophers to the north and west [*Geomys bursarius bursarius*], and the southern populations of *missouriensis* were identified as *Geomys lutescens*, although there is at least a 200 mile gap between these and the nearest populations of *Geomys lutescens* in northeastern Oklahoma. Additional specimens of both the pocket gophers and lice are needed to clarify this problem. Pocket gophers in southern Missouri apparently are restricted to "islands" of prairie within the Oak-Hickory forest (*Quercus-Caraya*), but little is known concerning the present distribution and habitat requirements of these pocket gophers.

Southern Group

A) *Geomydoecus heaneyi*--This louse is found on only two subspecies of pocket gophers, *Geomys lutescens llanensis* and *Geomys lutescens texensis*. These two pocket gophers occur in the Central Basin, a restricted area of the Edwards Plateau of central Texas. The Central Basin is a relatively small region with sandy clay and sandy loam soils (Pedernales and Tishomingo soils, see Carter, 1931), which support a Mesquite-Oak savanna (*Prosopis-Quercus-Andropogon*) vegetational community. *Geomys lutescens texensis* is found in a limited area in Mason and McCulloch counties and *Geomys lutescens llanensis* is found just to the east in a restricted area of Llano and San Sabo counties (Dalquest and Kilpatrick, 1973). Pocket gophers in the Central Basin are isolated from other populations of *Geomys* by clay soils that are unsuitable for *Geomys* and by the Colorado River (Davis, 1940).

Historically, the taxonomy of these two pocket gophers could best be described as unstable, in part because of striking differences in cranial morphology despite close geographical proximity. *Texensis*, first described as a distinct species (Merriam, 1895), was reduced to a subspecies of *Geomys breviceps* by Davis (1938). *Llanensis* was first described as a subspecies of *Geomys breviceps* by Bailey (1905), who stated that "While closely resembling *texensis* externally ...it needs but a cursory examination of the skulls to show that this form has no connection with that species." Davis (1940) transferred *llanensis* to a subspecies of *Geomys lutescens*. Later, *lutescens* was assigned as a subspecies of *Geomys bursarius* (Villa and Hall, 1947). Baker (1950) found what he considered hybrids between *texensis* and *llanensis*, so transferred *texensis* from the *Geomys breviceps* group to *Geomys bursarius*. Hence, both *llanensis* and *texensis* are classified

today as subspecies of *Geomys lutescens*. Hart (1978) examined the karyotypes of both subspecies and found them to be similar (2N of 70-72, FN of 68-70 and all chromosomes acrocentric). He suggested that this group was possibly derived from *major*. *Geomydoecus heaneyi* is a very distinctive louse and this implies, as does the distinctive cranial morphology and karyotype data, that these two subspecies of pocket gophers have been genetically isolated for some time from the neighboring populations of other pocket gophers.

B) *Geomydoecus subgeomydis*--This species of louse is found on two taxa of pocket gophers, *Geomys attwateri* and *Geomys breviceps sagittalis*.

The population of pocket gophers now referred to as *Geomys breviceps sagittalis* was originally described as six different subspecies (*sagittalis*, *brazensis*, *dutcheri*, *ludemani*, *pratincola*, and *terricolus*). As a result of a morphometric and chromosomal analysis, Honeycutt and Schmidly (1979) concluded that the gophers of extreme southeastern Texas were best represented by recognizing a single subspecies, *Geomys [bursarius] sagittalis*, with a second taxon, *attwateri*, found to the west.

C) *Geomydoecus ewingi*--This species of louse is found on three taxa of pocket gophers, *Geomys attwateri*, *Geomys breviceps breviceps*, and *Geomys breviceps sagittalis*. The presence of *Geomydoecus ewingi* on *Geomys breviceps breviceps* supports Honeycutt and Schmidly's (1979) conclusion that *breviceps* is most closely related to *sagittalis*.

The geographic distribution of *attwateri* and *sagittalis* is in close, but not perfect, agreement with the boundary between the two species of lice, *Geomydoecus subgeomydis* and *Geomydoecus ewingi* (Timm and Price, 1980). In general, *Geomydoecus ewingi* is found on the eastern subspecies, *Geomys*

7) There is a distinct division between the southeastern subspecies (*attwateri-breviceps-sagittalis*) and the northern group (*knoxjonesi-lutescens-major*).

8) The northern *Geomys lutescens lutescens* (north of the Platte River) are distinct from the populations of *Geomys lutescens lutescens* south of the Platte River.

Role of Dispersal in Fahrenholz's Rule and Resource Tracking

Students of Mallophaga have long been puzzled by the following facts:

1) Frequently an individual bird may be parasitized by several species of Mallophaga, whereas in mammals it is uncommon to find more than one species of chewing louse on an individual.

2) Closely related species of mammals almost always are parasitized by closely related species of Mallophaga (Fahrenholz's Rule), whereas in birds this is only the case sometimes; frequently there is no evidence of close phylogenetic parallelism between birds and their parasites.

This difference between mammals and birds in speciation of their parasites is seen not only in the Mallophaga, but also in the parasitic mites. It was this lack of phylogenetic parallelism in quill mites (Syringophilidae) that led Kethley and Johnston (1975) to propose the Resource Tracking hypothesis.

In attempting to test the Fahrenholz's Rule and Resource Tracking hypotheses, I saw parasite dispersal rates as the most important single unknown factor once thorough taxonomic studies of both the host and parasite had been conducted. The unstated, but underlying assumption, behind Fahrenholz's Rule model is that there is no dispersal of parasites between unrelated hosts (or that dispersers do not survive). The unstated assumption behind the Resource Tracking model is that

there is some opportunity for each species of parasites to disperse to and colonize any given host.

Dispersal (or the lack of dispersal) of individuals between populations is a primary factor in the speciation process. Wright (1931) has calculated that a dispersal rate as low as one individual per year between populations is enough to prevent genetic divergence (with no selection). If selection pressures are similar, a dispersal rate much less than one per year would be sufficient to maintain the genetic coupling of the two populations, and prevent speciation of lice on different host species.

Because the two models are based on conflicting assumptions concerning dispersal, the important question becomes whether dispersal of parasites among birds is different from that among mammals? Although few quantitative data on dispersal of Mallophaga are available, we do have some anecdotal information that can be evaluated.

We can assume that dispersal of lice from a female host to her offspring is commonplace, and that parasites readily disperse between adults during copulation, communal roosting, huddling, etc. Thus, there is ample opportunity for dispersal and mixing of the gene pool of parasites between different members of a single host species. However, transfer of parasites between different species of hosts presents additional problems. First, lice are extremely specialized for an ectoparasitic mode of life. They are wingless with legs highly modified to cling to either feathers or to fur, but not to walk on other substrates. Second, lice can not live long once removed from their hosts; Askew (1971, p. 21) wrote that "Lice generally are very sensitive to temperature and most soon die when their host's body cools after death."

How then can Mallophaga disperse to other species of hosts? It has been known for more than a century that

Mallophaga are sometimes found attached to hippoboscid flies (Diptera: Hippoboscidae). There are some one hundred species of hippoboscids world-wide; most are parasitic on birds, although a few parasitize large mammals. In general, hippoboscid flies are not host-specific; a single species of hippoboscid can be found on numerous families of birds and even on birds of different orders. Hill (1962) has shown that several species in the genus *Ornithomyia* select for size classes of birds or for birds of given habitats (woodland birds, moorland birds, etc.) rather than for closely related hosts. Most species of hippoboscids have wings and can fly readily. The lice cling to a fly by grasping a leg or wing with their mandibles; they are transported by the fly to a new host. This mode of transportation, termed phoresy, was defined by Farish and Axtell (1971, p. 17) as "a phenomenon in which one animal actively seeks out and attaches to the outer surface of another animal [phoriant] for a limited time during which the attached animal (termed the phoretic) ceases both feeding and ontogenesis, such attachment presumably resulting in dispersal from areas unsuited for further development, either of the individual or its progeny."

Phoresy by Mallophaga on hippoboscids is considered accidental or rare (Ansari, 1947). In a review of phoresy by Mallophaga, Clay and Meinertzhagen (1943) reported 13 new cases of lice being attached to some 200-300 hippoboscids they examined, and commented that these were "meager results." However, this magnitude of dispersal (0.5% of the flies they examined) is high when considered over evolutionary time. In recent reviews, Keirans (1975a, b) summarized records of 416 cases of phoresy, but felt that the only survival value for the lice involved would be if the hippoboscid fly transported it to another member of its host species. It has been noted that, when hippoboscid flies are carrying Mallophaga,

frequently they have more than one (44% had two or more) (Clay and Meinertzhagen, 1943), and one fly was recorded with 31 lice (Peters, 1935). Clay (1949) suggested that phoresy on hippoboscids may have played an important role in the speciation of Mallophaga. It seems likely that phoresy on hippoboscid flies could have been a major factor in interspecific transfer of Mallophaga among birds. An interesting phoretic relationship has been suggested between bat fleas (*Lagaropsylla turba*) and ectoparasitic earwigs (*Arixenia esau*), both host-specific to the naked bat (*Cheiromeles torquatus*) (Marshall, 1977a,b; 1982). The eggs and larval stage of the flea are found in the bat guano on the floor of caves. Bat fleas are poor jumpers, and it has been suggested (Hutson, 1981) that the adult fleas reach the bats on the ceiling of the cave via transport by earwigs. Marshall (1977) found that 69% of the earwigs examined (201) carried fleas, with up to 40 fleas found on individual earwigs.

The feathers may be a second mechanism for interspecific transfer of bird ectoparasites. A considerable number of species of birds incorporate feathers of other birds into their own nests. This is especially true for the passerines. Bird feathers are also frequently incorporated into the nests of mammals, especially rodents. Thus, a founder population of a single female or even an unhatched louse egg on a loose feather may be deposited in the nest of a foreign host. If it is able to feed and reproduce on the new host, a successful transfer will have occurred.

A third mechanism for interspecific transfer of Mallophaga is communal use of dust baths (Clay, 1949; Hopkins, 1949b; Hoyle, 1938), but this mechanism is untested.

A fourth mechanism for interspecific transfer of bird ectoparasites may be in multiple use of holes for nesting. Cavities are a limited and highly prized resource for nesting.

A given cavity will host a successive array of species of birds throughout the nesting season and some birds will even expropriate other bird's nests (Welty, 1982). A parasite in the nest would find its host replaced by another species.

The opportunity for exchange of lice between different species of birds clearly exists. It is likely that the vast majority of interspecific exchanges do not survive, but because a single gravid (or parthenogenetic) female louse may give rise to populations on a new host, it seems likely that this sort of dispersal has produced the distribution patterns described as Resource Tracking. It is apparent that, in general, bird ectoparasites have more opportunities to reach a foreign host than do some groups of mammal ectoparasites.

In addition to the differences in dispersal opportunities for bird and mammal ectoparasites, birds and mammals differ in the complexity of niches available to the ectoparasites. Mammalian hair is relatively simple and uniform to lice, whereas avian feathers are complex in structure and variable across the body. Thus, parasites have several niches open to them on a single bird. The specialized niche provided by down, contour feathers, filoplumes, or the inner pulp cavity of the shaft may be more similar as a niche between closely related species of birds than they are among each other on the same bird. Cornell and Washburn (1979, p. 257) stated that, "parasite species richness asymptotically approaches an upper limit established mainly by host 'island' size and that recent evolutionary age has an insignificant effect on the number of species which attack the host." Birds constitute a "larger" island for colonization by parasites because of their diversity of niches available. The habitat richness on birds thus supports species richness of ectoparasites.

Successful transfer of lice between different taxa of birds is a rare event, but the probability of transfer of

lice between taxa of pocket gophers of the genus *Geomys* is an exceedingly rare occurrence. Thus, the species of Mallophaga on *Geomys* represent a lineage that has evolved in parallel to the pocket gophers (Fahrenholz's Rule), and the relationships of the lice may be an extremely useful tool in elucidating the relationships of the pocket gophers. Fahrenholz's Rule and Resource Tracking are not conflicting hypotheses. Rather, they apparently represent the ends of a continuum based on dispersal opportunities and niches available to the parasite.

ACKNOWLEDGMENTS

I thank Hugh H. Genoways, Robert S. Hoffmann, James L. Patton, David J. Schmidly, and Henry W. Setzer for allowing pocket gopher skins under their care to be brushed for lice; Elmer C. Birney, Barbara L. Clauson, Edwin F. Cook, Lawrence R. Heaney, L. Henry Kermott, John B. Kethley, Ke Chung Kim, Matthew H. Nitecki, Bruce D. Patterson, Roger D. Price, and Rupert L. Wenzel provided helpful discussion and comments on the manuscript, and Rosanne Miezio illustrated the pocket gopher and skull. Special thanks are to Barbara L. Clauson, Lawrence R. Heaney, and Roger D. Price for assistance on various aspects of this project.

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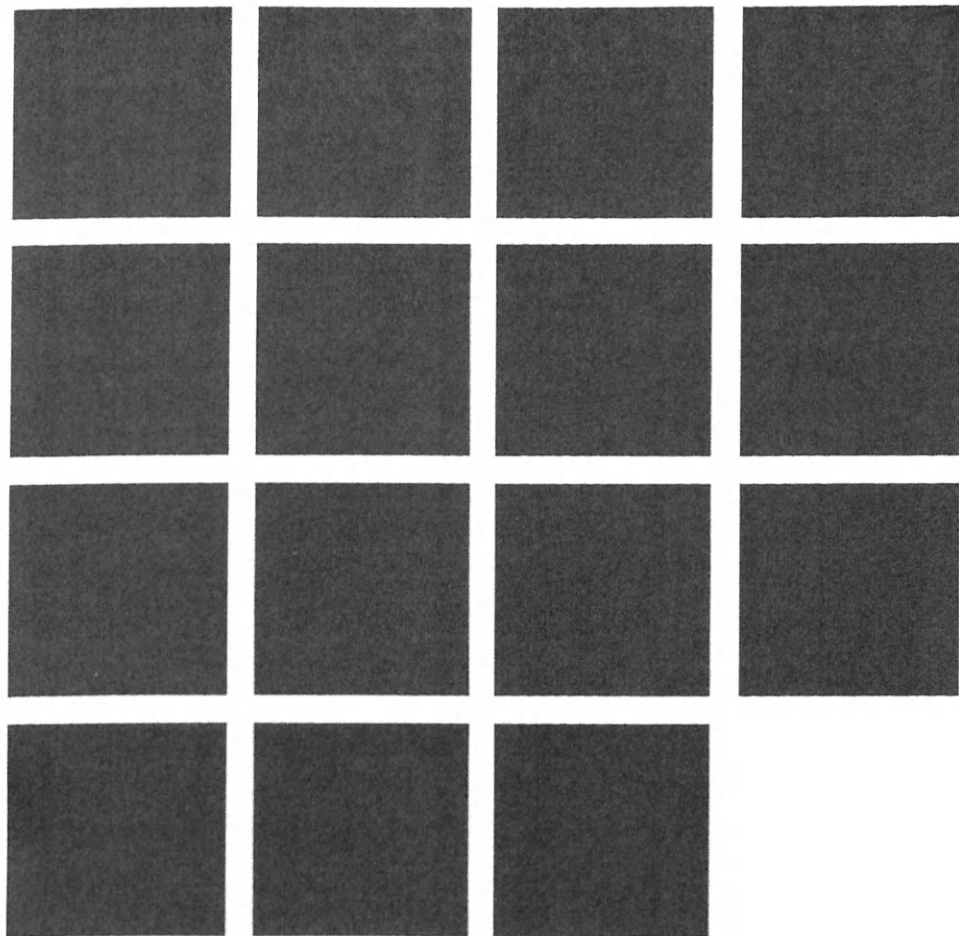
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Edited by
Matthew H. Nitecki

The University of Chicago Press
Chicago and London

